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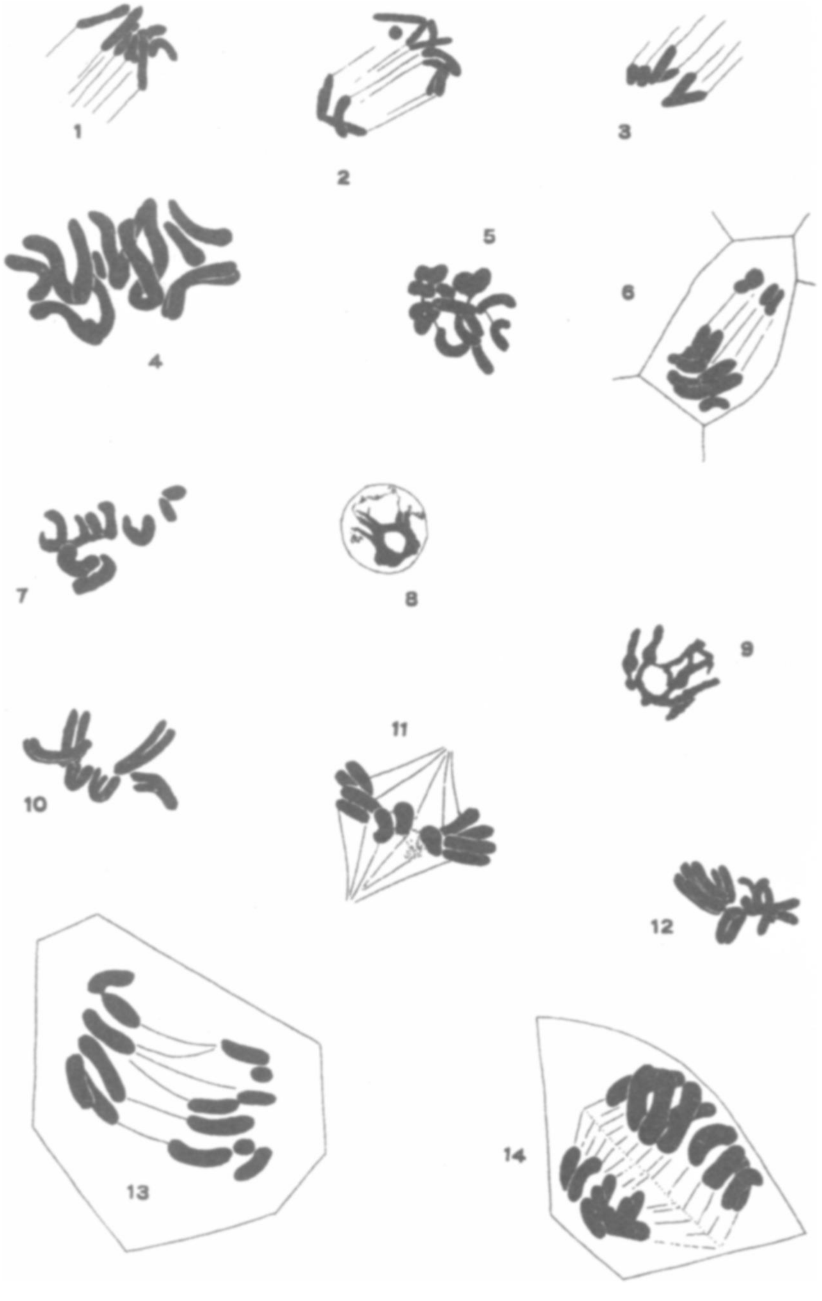

SPERMATOGENESIS OF HYBRID PEAS.

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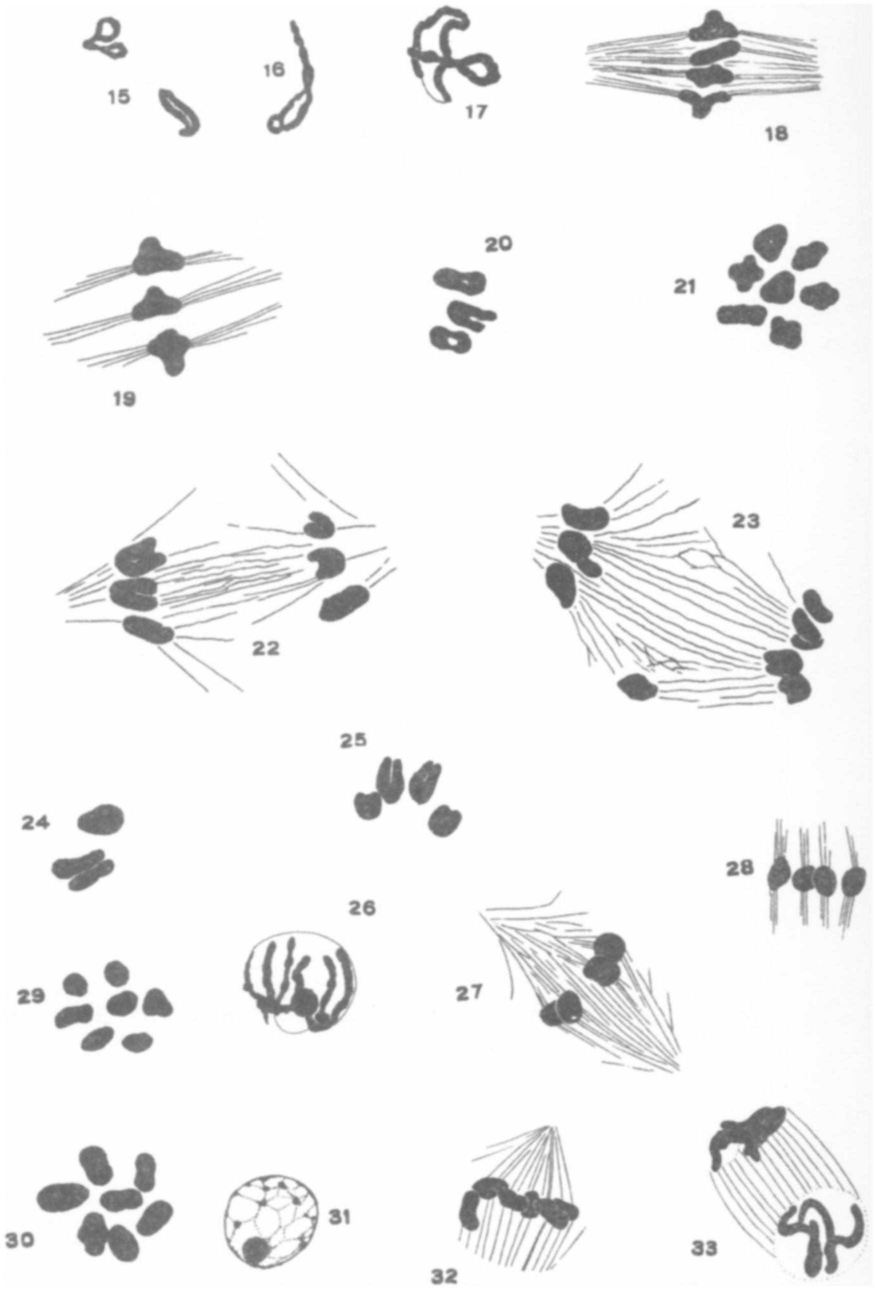

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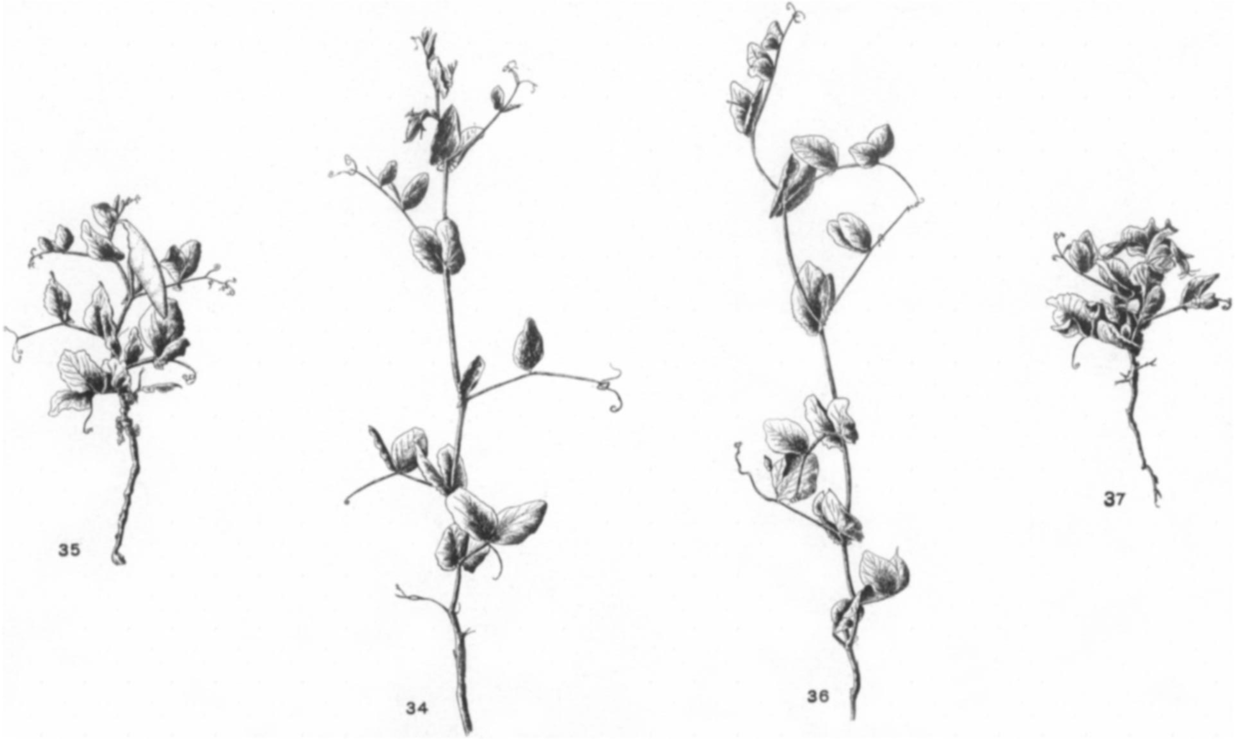

STUDIES IN PLANT HYBRIDS: HYBRID PEAS

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Studies in Plant Hybrids: The Spermatogenesis of Hybrid Peas*

BY WILLIAM AUSTIN CANNON

(WITH PLATES 17–19)

Up to the present the studies on the origin and development of the spores and sex-cells of hybrids have been made with no definite knowledge of the manner of the variation of the hybrid race and without regard to or accurate knowledge of the degree of fertility or sterility of the forms, and it seems almost unnecessary to remark that no study can be at all complete, whatever its results or conclusions may be, that does not take into consideration each of these conditions.

Studies on the sporogenesis and spermatogenesis of hybrids include the researches on cannas by Guyer,† on cotton by Cannon, on *Drosera* by Rosenberg, on *Gladiolus* by Metcalf, on pigeons by Guyer and on *Syringa* by Juel. Nothing definite is known, so far as I am aware, about the variation of any of these hybrids, and as regards their fertility probably not one is entirely fertile, and *Syringa* at least is thought to be quite sterile.

There are two or three conditions at least to which a hybrid plant should conform in order to be well adapted for study from a morphological standpoint. These are briefly: the hybrid must be fertile; it must vary in a definite and known manner; and, finally, it must be suitable in itself, as distinguished from all other requirements, for histological study.

One reason why the pea hybrids are so well adapted to experimental researches is that they are fertile. This, indeed, was one of the reasons that led Mendel to select them for his studies. I

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* This study was made with the aid of Grant No. 27 of the Carnegie Institution.

† See bibliography at the end of this paper.

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have observed also that the peas used in the present study were fertile; they produced pods which were usually well filled with seeds capable of germination. These observations are in harmony with the manner of the formation of the spores; no irregularities whatever, which in any way were traceable to the plants as hybrid organisms, were seen. If these observations are correct, the conclusion can hardly be avoided that the variations and reversions of hybrid peas are associated with normal processes, such as are found in the pure types, and hence that abnormalities are merely indications of the hybrid nature of the forms that bear them, although by no means diagnostic characters. It is then a question fairly open for the cytologist to determine, what the nature of those processes are, and this has yet to be done.

The hybrids used in this study,* Fillbasket x Debarbieux and Express x Serpette, showed variation after the law of Mendel, although I should state that they were not examined more than was necessary to surely establish this point. The seeds from which the plants studied were derived were from those of the first generation. The Fillbasket x Debarbieux seeds were yellow and green, nearly in the ratio 3 : 1. Of course most of the flower-buds were removed for study, but in a few cases I left the flowers to fertilize themselves. The plants which came from the green seeds bore green seeds only, and those from the yellow seeds bore seeds that were both yellow and green in the ratio 3 : 1. In the crosses in which Serpette was used as one of the parents, as for example Express x Serpette, the Serpette dwarf character was noticed in the offspring as presumably the recessive one; it appeared in at least one third to one half the total number of third-generation plants. In Express x Serpette there were seventy-two plants which resembled the Express ancestor, and thirty which were dwarfed and which were like the Serpette race. The illustrations (*f. 34–37*) show fairly well the appearance of these reversionary types and the pure forms also.

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*I am indebted to Professor William Bateson for the seed from which the hybrids were raised. Professor Bateson very generously sent me some first crosses, several of the second generation and also the pure types.

I wish also to acknowledge the assistance of Mr. Homer D. House, of Columbia University, for aid in preparing material for study, and that of Miss Palmyre de C. Clarke, of the New York Botanical Garden, who prepared the bibliography.

FILLBASKET AND DEBARBIEUX, PURE RACES

No difference in the origin and development of the microspore was noted between the pure races Fillbasket and Debarbieux. In both the reduced number of chromosomes was seen to be the same, namely seven, and the chromosomes appeared to be quite alike in each ; to avoid repetition the general account of the maturation processes will be deferred until the next topic. Favorable material, however, gave opportunity to observe the sporogenous divisions in Fillbasket and the results are here presented.

In the most of the sporogenous divisions the mitotic figures are likely the same as in the somatic nuclei ; but in late anaphases or early telophases certain characters were seen which were apparently somewhat different. In early telophase of one of the later sporogenous divisions the chromosomes are associated in pairs, touching by one, the polar, end. A nucleus with such chromosomes is shown in *f. 4*. This division was evidently the last sporogenous one, that is, the nucleus figured would become that of the spore mother-cell without further division. Whether the chromosomes are ever in touch throughout their whole length, as appears to occur in Fillbasket × Debarbieux (*f. 6*), was not determined. The later history of the chromosomes is of great interest, since upon a proper understanding of it may depend an appreciation of the significance of the loops of chromatin which appear subsequently in the nucleus as one of the prophases of the first maturation division. If, as supposed, the spireme of the nucleus of the spore mother-cell is double, we might look for a previous doubling of the chromosomes, although this might perhaps not follow. I have seen no clear indication that the chromosomes form a double spireme in the telophases of the last sporogenous division. The behavior of the chromosomes at this time is as follows : As they approach the poles of the spindle they are appreciably more uniformly arranged and more nearly parallel to the long diameter of the spindle than in the other divisions in the sporogenous cells, when at the poles the chromosomes unite or touch two and two by the polar ends. In this condition they enter the resting stage ; a continuous spireme was not seen. In some nuclei the adjoining pairs of chromosomes were apparently united by their free ends, but I did not surely determine this point. If the chromosome pairs are united in this manner a continuous spireme of single chromosomes united end to end would be the result. The results of my observations upon this point were somewhat contradictory, and this may have been owing to the possibility that not all of the nuclei studied were undergoing the last sporogenous division, and that the pairing of the chromosomes and the form of telophase following are, in the pea, peculiar to the presynaptic nuclear division. I hope at another time to give a more complete account of this division.

When I observed the association of chromosomes as above described I supposed that it was merely from chance, which indeed may yet prove to be the case, and not the usual and normal occurrence in such cells, because it surely is not at all likely that so noticeable a thing could for any length of time escape the eyes of trained cytologists. The better to reinforce the correctness of my observation, or to prove it false as the case might be, I studied the mitoses in the nuclei of somatic cells. As a rule, there is no indication whatever in the somatic nuclei of peas of the association of the chromosomes in twos, but in one nucleus an appearance recalling the pairing was observed. In this case a closer examination showed that the association did not include all of the chromosomes and was very evidently one of chance merely; so that it seems to me that the association of the chromosomes in pairs in the last sporogenous division in Fillbasket does not find a counterpart in any somatic cells and is not the result of chance.

FILLBASKET × DEBARBIEUX

In studying the sporogeny of the hybrid Fillbasket × Debarbieux my aim has been rather to notice departures from the "normal," and by it to discover if possible the structural causes of the remarkable "splitting" of the Mendelian hybrids, than to examine critically and minutely the several nuclear divisions for themselves. Accordingly I have observed the behavior of the chromosomes more especially in the two maturation mitoses, in the first division of the microspore and in the last division of the sporogenous cells.

The sporogenous cells of the hybrids were rather easily distinguished even in young anthers because of their position and by the greater density of the cytoplasm, although it should be said that it is not seldom difficult surely to determine the character of a given cell. To study the divisions from which the sporiferous tissue arises it is necessary to obtain very young anthers indeed, those which are merely slight protuberances on the primordium of the flower. The difficulties in the way of studying the anther are decidedly increased from the fact that the inflorescence consists of not more than four or five flowers, all usually in widely different stages of development.

For the most part the nuclear divisions in the sporogenous cells of Fillbasket x Debarbieux are of the regular equational type, quite the same as those in the somatic cells of the plant. That is, fourteen segments are formed in the prophases and these become arranged in the equatorial plate and in metaphase are already split before the migration to the poles of the spindle. In anaphases the chromosomes are frequently L-shaped, although not so sharply bent, and are arranged haphazard, that is, as purely by chance. In the telophases the chromosomes unite end to end and form a spireme; this becomes changed into a delicate reticulum in which all trace of the chromosomes as such disappears.

In some of the later sporogenous divisions a departure from the usual appearance was noted as in the case of the pure form Fillbasket. In Fillbasket x Debarbieux the same curious association of chromosomes two and two was observed in a few cases. *F. 6* shows an anaphase of the last sporogenous division; the pairing was even more clearly marked in the preparation than in the sketch. The pairing was with a single exception observed in anaphase or early telophase only. The exception is shown by *f. 5*, which is an equatorial plate in probably the last division before synapsis. I have not seen the association in early anaphase for the reason perhaps that the chromosomes are at that time under the influence of the spindle fibers.

When the chromosomes reach the poles of the spindle they unite by their polar ends, and these appear to fuse together, making a more or less well-marked ring from which depend the chromosomes in pairs. This is shown very imperfectly by *f. 7, 8* and *9*. In no case did I see a spireme which I could surely say was continuous or which was made up of more than two elements; this may well be because the particular stage was wanting in the preparation. On the other hand instances were observed, like *f. 8*, in which a reticulum was being formed from the condition as just described. The exact fate of the chromatin was thus not determined.

The association of chromosomes in pairs in the early history of the reproductive cells recalls the similar condition in animals as given by Montgomery * and Sutton.† But the significance of the association in hybrids is not entirely clear, since with Montgomery's hypothesis in mind that in pure races the two chromosomes of each pair are of different parentage, it seems difficult to conceive of Sutton's as applied to hybrids, that the members of each pair cover the same field of development; because in hybrids the latter can only be true in a broad way, depending apparently upon the affinities of the pure parents of the form. It may be, however, that the differences between the chromosomes of any pair in hybrids capable of forming functional spores are so slight that union is possible even if the potentials of the chromosomes are not identical.

After the sporogenous cells are cut off there ensues a long period of growth during which the nucleus of the young spore mother-cell undergoes characteristic changes. The chromatin of the nuclear reticulum becomes gathered to one side of the nucleus and the contracted condition known as synapsis results. The preparation for synapsis takes place at an early time in the history of the spore mother-cell, and the portions of the nuclear changes resulting in synapsis which were seen may be briefly described. The delicate reticulum which extends through the nuclear vacuole of the resting nucleus becomes so changed that small masses of chromatin of unequal form and size are found scattered along its meshes, more especially in the peripheral part of the nucleus. These masses are arranged in lines which often radiate from the nucleolus as a center; the linin threads which connect the masses may be seen for a considerable distance from them extending into the nuclear vacuole. From a position extending over the entire periphery of the nucleus the chromatin becomes gathered to one side of the vacuole; when it enters into the synapsis stage it is probably already in the form of a continuous spireme. It is much bent with short turns and appears usually to be homogeneous and not split; the spireme at this time closely resembles the much convoluted thread with its short, sharp turns as it emerges from the synapsis stage. Since the chromatin assembles in a spireme before the so-called synapsis condition the significance of the latter is not apparent in these forms.

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* Montgomery, T. H. The heterotypic maturation mitosis in Amphibia and its general significance. Biol. Bull. 4: 259. 1903.

† Sutton, W. S. On the morphology of the chromosome group in *Brachystola magna*. Biol. Bull. 4: 24. 1902.

The cytoplasm of the spore mother-cell is reticular and it always, from the spore mother-cell to the tetrad, retains this structure. In this regard the pea is very different from the cotton hybrid in which kinoplasm forms a marked character of the cytoplasm in the more advanced stages of spore formation, and from some of the homologous cells of *Syringa Rothomagensis* * in which kinoplasm is strongly developed. The exaggerated development of kinoplasm or filar-plasm in the cytoplasm of the spore mother-cells is therefore not a constant or diagnostic feature of hybrids.

Although I did not study closely the origin of the achromatic figure, I observed that it is derived from a multipolar one. The multipolar-spindle originates in groups of fibers which are placed near the outer edge of the cytoplasm and which radiate from a common point towards the nucleus. The place of genesis of the achromatic figure is therefore very different from that of the cotton hybrid, and the structural reason appears to lie in the presence in the latter, and absence in the former, of a dense perinuclear zone of cytoplasm. The achromatic figure in cotton originates inside of this perinuclear zone, which thus appears to inhibit its more peripheral origin. It may also be that the zone of denser cytoplasm which in the cotton closely surrounded the nucleus not only formed a limiting boundary for the spindle, but at the same time made necessary for the mechanical support of the cell the formation of an outer layer of kinoplasm, and that its absence in the pea not only changed the structural relations of the parts of the cell but altered the mechanical condition as well, making the formation of the kinoplasmic layer unnecessary.

The first maturation mitosis is heterotypic. The chromosomes in the metaphase are not different from those in the pure races Fillbasket and Debarbieux. Their relatively large size and small number make the observation of them comparatively easy and sure. The reduced number is seven; this number was repeatedly seen in the first division and was verified in the second mitosis and in that of the division of the nucleus of the tetrad also.

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* Juel, H. O. See bibliography.

The chromosomes in the anaphases of this division are more or less bent and some show the splitting sometimes seen in these stages of division. There was an equal apportionment of the chromosomes, both as regards their number and size, to the daughter nuclei. The single exception to this, and the only abnormality noticed in the hybrids, is shown in *f. 23*. In the nucleus from which the sketch was made one chromosome lagged behind its companions; fission, also, had not taken place.

The daughter nuclei undergo reconstruction to a greater degree than was observed in the cotton hybrid, but on account of the small size of the nuclei the study of them is difficult and unsatisfactory. The chromosomes in early telophase are much elongated and appear to unite end to end to form a single spireme, which later becomes lumpy and more or less reticular. The identity of the chromosomes is quite lost.

In the prophases of the second division a spireme, which does not seem to be split, may be seen, and the chromosomes formed from it become associated in pairs in the nuclear plate, but they may not on that account, as Mottier shows, be sister chromosomes. It is probable, however, that they are, and that they are not homologous with the pairs found in the presynaptic division. The metaphase or the anaphases present no noteworthy condition. The reduced number of chromosomes, seven, was frequently observed and the number verified.

In late anaphases of the second division the cell-plates separating the daughter nuclei may be seen, and when the granddaughter nuclei are reconstructed cell-division occurs. Immediately after the division of the cell the tetrads are angular in form, but they soon become spherical and at length they assume the elliptical form characteristic of the pollen-grain. During these changes in form the tetrad increases much in size and the nucleus of the young spore moves from its early central position to one end of the cell and there prepares for the division of the nucleus of the microspore.

The first division of the nucleus of the spore (*f. 32*) appears to be similar to that of the somatic nuclei except for the number of the chromosomes and the shape of the spindle. The chromosomes are of course the reduced number, and the spindle, owing perhaps to the eccentric position of the nucleus, is somewhat truncated. As in the two preceding divisions, the distribution of the chromosomes in this one was apparently perfectly equable. Therefore in all and in each of the nuclear divisions which were directly connected with the development of the microspores the number of the chromosomes, and also presumably the amount of chromatin, were equally distributed.

In late anaphase of the first division of the nucleus of the microspore a cell-plate is seen separating the crescentic-shaped generative nucleus from the vegetative one. Reconstruction of the two nuclei goes on at an unequal rate. The vegetative appears always to form its wall in advance of the sister nucleus, and its chromosomes are also the first to become reticulated and lose their identity. In the reconstruction of both nuclei excellent opportunity was given to observe the beginning and extension of the nuclear wall, which appear to occur precisely as Lawson has described.*

SERPETTE, PURE RACE.

The material of the pure parents of the Express × Serpette hybrid at my disposal was not sufficient to permit an extended study of either; but some observations were made on the critical stages of spore-formation in Serpette.

The first maturation division in Serpette is heterotypic and the second homotypic. In the anaphases of the first division the chromosomes were not seen to be split, either for part or all of their length, as was the case in the other pure races and the hybrids also. In the telophases of the daughter nuclei the chromosomes unite end to end and form a continuous daughter spireme. In both maturation mitoses the reduced number of chromosomes was seven. No differences in form or size were noticed between the chromosomes of this and those of the other pure races.

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* Lawson, A. A. On the relationship of the nuclear membrane to the protoplast. Bot. Gaz. **35**: 305. 1903.

EXPRESS × SERPETTE

Like Fillbasket × Debarbieux, this is a second generation hybrid, and it also, as has been described in a preceding paragraph, shows the splitting into several types after the law of Mendel. The reversion of Express × Serpette as regards the quality of size and form of the plants is fairly well indicated by *f. 34–37*, where the pure parents are also represented. It should be noted that the sketches are drawings from photographs and that the plants were photographed at the same time and under precisely the same conditions, so that the figures faithfully reproduce the relative forms and sizes of all of the plants.

The sporogeny of Express × Serpette corresponds closely in the points examined to that of Fillbasket × Debarbieux, although in certain regards, which will be indicated, a difference between the two was noted. Also some phases of development were represented in my preparations of Express × Serpette, not found in those of the other hybrid, and these will be mentioned, in addition to the preceding, rather than a more complete account. By this method I shall avoid unnecessary duplication; the two hybrids are so nearly alike in the matter of spore origin and development that a description of these processes in the one would for the most part answer perfectly well for the other.

The series representing the nuclear divisions in young anthers was not so complete in Express × Serpette as in Fillbasket × Debarbieux, and possibly for this reason I have not so complete evidence of the association of the chromosomes in pairs in the last sporogenous division in the former as in the latter hybrid. It was observed, however. An apparently good example of the pairing was seen where perhaps one would not expect it, namely, in the division by which the sporangial wall is separated from the inner sporiferous tissue. The outer cell resulting from this division by further division gives rise to three series of cells, the inner of which forms the tapetum; the inner cell of the division noted becomes converted without further division into a spore mother-cell. The division referred to occurs rather late in the pea. Both of the nuclei resulting from this division had their chromosomes arranged in twos. If the curious association of the chromosomes is an especial preparation for synapsis, the condition of the outer one is surely paradoxical.

The nucleus of the spore mother-cell enters into a complete resting condition in which it remains during much or most of the period of growth of the cell. As a preparation for synapsis the chromatin of the recticulum collects into masses of irregular shape and size, more or less arranged in threads, about the periphery of the nuclear vacuole. The chromatin-thread at length takes up a position around or closely applied to the nucleolus and the synapsis stage results. When the mass of chromatin unloosens, it is seen to be made up of a much bent ribbon. The spireme is at first beaded in appearance, but it becomes more regular in outline and also increases in its capacity for absorbing stains. The splitting of the spireme was not clearly seen, although evidences of it were noticed. In a few cells I saw the chromatin-loops which are characteristic of the prophases of the first maturation mitosis (*f. 15–17*), but in each case the loop was not contracted and did not show the second fission which was observed in the cotton hybrid.

The two maturation divisions were quite like those seen in Serpette and in Fillbasket x Debarbieux. The reduced number of chromosomes was seven.

A difference in the origin of the multipolar spindle of the first mitosis of Express x Serpette from that of Fillbasket x Debarbieux was noted (this stage was not seen in Serpette), but whether it was an artefact or not I was unable, because of the lack of material, definitely to determine. In several spore mother-cells the cytoplasm was very dense in the immediate neighborhood of the nucleus, forming what was in effect a perinuclear zone. In these cells the multipolar spindle seemed to have its origin wholly within the nucleus. The linin became lumpy and very distinct, it formed a mesh-work which gave the appearance of polarity, and had every indication of being the genesis of the multipolar spindle. The nuclear wall remained in some cases recognizable even when the intranuclear material was of a pronounced fibrous character. The departure from the extranuclear origin of the spindle observed in Fillbasket x Debarbieux is certainly a marked one, and interesting even if it proves in the end to be an artefact.

SUMMARY

The main points in this paper may be briefly stated as follows:

1. Both of the hybrids studied and reported on in this paper, Fillbasket × Debarbieux and Express × Serpette, were of the second generation, that is, their grandparents were pure races of peas; both of the hybrids exhibited variation after the Mendelian law.

2. The hybrids are fertile.

3. Both of the hybrids matured their spores quite as the pure ancestral forms did. The first maturation mitosis was heterotypic, the second homotypic.

4. The reduced number of chromosomes is seven, the somatic number fourteen.

5. No abnormal mitoses were observed.

6. In the anaphases of the last sporogenous division of both hybrids, and of the pure form Fillbasket, the chromosomes were associated in pairs; this condition was seen also in one nucleus of Fillbasket × Debarbieux that was in the nuclear plate stage. The paired condition is probably not the result of chance; further work, however, which the writer hopes to carry on, will be necessary definitely to determine this point.

CONCLUSIONS

If the physical basis for the Mendelian variation of hybrid peas was not demonstrated by a single histological study of them, certain conclusions which touch more or less directly the causes of the variation may nevertheless be legitimately although tentatively drawn. In the first place it has been shown that the variation of the peas, in the third generation at least, is due entirely to the union of gametes which originate and develop quite the same as do those of the pure ancestral types, or in other words, abnormalties and irregularities of nuclear divisions do not form the basis for the variation of these hybrids.

What then is the probable structural basis for the Mendelian variation of the hybrid peas? As has already been intimated, I think it is fairly well shown that this basis is the same as that of the variations in the pure forms, and if so an understanding of the latter should give the key to explain the former as well. But nothing is clearer than the fact that the present conception of the essential nature of the maturation processes in pure races of plants does not provide adequate grounds for this variation. This study will hardly profess to do this, but I may repeat what I have before suggested * and what Montgomery † and Sutton ‡ have emphasized, that a study of the early history of the reproductive cells may give some clue leading to a better understanding of the meaning of heterokinesis, and, at the same time, a truer conception of the physical basis for variations, both in pure races and in hybrids. With this idea in mind I have studied, as well as the material at hand would permit, the divisions of the sporogenous cells, more especially the last one, the division preceding the first maturation mitosis, in the hybrids and in the pure form Fillbasket, and I have found unmistakable evidence of an association of the chromosomes two and two. Of course I cannot say positively that this was not a chance association, since I could not trace the later phases of these divisions as closely as would have been desirable, but the pairing was observed in well prepared material and had every appearance of being the normal and regular occurrence. If further studies confirm this observation, it may prove of great importance in explaining the structure of the heterotype rings. There are difficulties in the way of positively identifying any chromatin loop as having its origin in any given pair of chromosomes, because the nucleus enters on a complete resting stage at the close of the presynaptic mitosis and the identity of the chromosomes is lost. Further studies may, however, give results that point to a connection between the two even if they do not make the demonstration. For example, I have seen the union of chromosomes by the polar ends only, in the telophases of the last sporogenous division, and I failed to find, although I searched very closely, the formation of a spireme, but in the place of it the *pairs* of chromosomes appeared to be united at the polar ends. A continuous spireme may not be formed in this division. It is conceivable therefore that the chromosome pairs which enter the resting condition may be identical pair for pair with the loops which are formed later.

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* Cannon, 2.

† Montgomery, *l. c.*

‡ Sutton, *l. c.*

Mottier * has described processes in the second maturation division which should be considered in connection with the earlier nuclear divisions as well. In the metaphase of the second division the chromosomes are brought into the paired position in the nuclear plate by the action of the fibers of the spindle; that is, the pairing here is probably due to the activity of the achromatic elements. This seems to make unnecessary the conception of the preliminary pairing of the chromosomes as a direct preparation for heterokinesis, since the spindle can distribute the chromosomes at its will, so to speak. It should be considered, however, that the rings are bivalent, and are probably formed without the intervention of the fibers, since the rings antedate the formation of the spindle itself. Also, if my observation is correct, the spindle fibers are not instrumental in segregating the chromosomes in the presynaptic division, because in that case, with possibly one exception, the pairing was not observed until the chromosomes were at the poles of the spindle and hence probably after the work of the fibers of that dividing nucleus was done. So it may well be that there is not only a difference in the homologies of the chromosome-pairs of the metaphase of the second division and those of the presynaptic one, but a difference in their affinities as well; consequently influences, whatever they may be, other than those of the spindle, may cause the earlier pairing.

The foregoing considerations are based upon the idea of the individuality of the chromosomes and upon that of their being qualitatively unlike.† If these conceptions are valid we should

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* Mottier, D. M. The behavior of the chromosomes in the spore mother-cells of higher plants, etc. Bot. Gaz. 35: 250. 1903.

† The results of Rosenberg's studies (see bibliography) on the sporogenesis of the natural hybrid between *Drosera longifolia* and *Drosera rotundifolia* seem to throw objections in the way of too strict a conception of the individuality of chromosomes in hybrid plants. Rosenberg finds that the reduced number of chromosomes in the *Drosera* hybrid may be 10, as in *D. rotundifolia*, or 20, as in *D. longifolia*, or 15, which is half the somatic number in the hybrid. He also finds some evidence indicating that part of the chromosomes may be made up of four portions of chromosomes each, and others of two halves of chromosomes each; the former kind are also larger. In any case it is difficult to reconcile Rosenberg's results with the idea that the chromosomes are distinct morphological entities; the results point rather to the preservation by a portion of the spores of the purity of the chromatin, a fact which may prove disconcerting to recent critics in this field (Cook; see bibliography). It should be

have spores which might be of pure descent or might not be so according to the manner of the orientation of the segments in the metaphase of the first division. The chromosomes might be associated and distributed by chance as I have recognized (Cannon, 1) and as Sutton has dwelt on at length.* What the connection of the chance distribution of the chromosomes may be with the distribution of the characters among the hybrids is not at all clear, since the relation of the chromosomes to the characters is not known, but the cytologist has abiding faith that there is some connection which will be demonstrable with the microscope, and he looks to the field of hybrids and of hybridization as a new opportunity for experimentation by which to supplement and to substantiate the results of his studies. Experimentation and cytological studies on hybrid forms in which the number of chromosomes is known and in which the number of characters has been determined should show a connection, if there is one, between the number of characters that are transmissible and the number of the chromosomes and their morphology. I wish here to call attention to what very likely is merely a chance coincidence, but nevertheless suggestive and interesting, namely, to the agreement in the number of the groups of constant differentiating characters as given by Mendel for the peas used by him in experiments with the reduced number of chromosomes in the peas. As given by Bateson (Bateson, 1), the characters are (*a*) differences in the length and color of the stem; (*b*) in the size and form of the leaves; (*c*) in the position, color and size of the flowers; (*d*) in the length of the flower-stalk; (*e*) in the color, form and size of the pods; (*f*) in the form and size of the seeds; (*g*) in the color of the seed-coats and cotyledons. In the peas there are evidently more appreciable characters than chromosomes, and therefore the chromosomes bear more than one character each. If then the chromosomes maintain their individuality certain characters might be associated together in the same chromosome, and might be

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borne in mind, however, that a difficulty in drawing conclusions at present from the results of Rosenberg's studies of the sporogeny of the *Drosera* hybrid may lie in the partial sterility of the form. (See Focke, Pflanzenmischlinge, 155.) Further work on this hybrid is promised and will be awaited with interest.

* Sutton, W. S. The chromosomes in heredity. Biol. Bull. 4: 231. 1903.

coupled together in the hybrid organism, not being capable of separating from each other — correlations are not unknown among hybrids. The idea suggests itself that the case might be very different if the number of the chromosomes in relation to that of the characters were greater than in the pea; the chance association and distribution of chromosomes representing portions of characters might not bring about so evident a distribution of characters in the hybrid generations, the Mendelian reversions. May it not be possible then that fortune favored Mendel when he selected for his experimentation plants which had so small a number of chromosomes? *

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LIST OF THE MORE IMPORTANT RECENT WORKS ON PLANT HYBRIDS

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* The data at hand showing the number of chromosomes in the somatic cells of Mendelian hybrids are unfortunately not complete. According to Wilson (The Cell, 206), in wheat there are 16 chromosomes, and in cattle and rats the number is probably the same; the mouse has 24 chromosomes; according to the present study the pea has 14. On the other hand, there are 56 chromosomes in the somatic nuclei of hybrid cotton, but the nature of the variations in the cotton, whether or not Mendelian, has not, I believe, been determined.

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Explanation of Plates

NOTE.—A Zeiss microscope with a 2.00 mm. homogeneous oil-immersion objective and a number 18 eye-piece were used, together with a camera lucida, in making all of the sketches in plates 17 and 18.

PLATE 17

FIGS. 1–3. Fillbasket, pure race. Anaphase of last sporogenous division: pairing of the chromosomes not well marked. The three sketches were made from one nucleus.

FIG. 4. Fillbasket, pure race. Late anaphase of the last sporogenous division. The chromosomes are uniting in pairs. One chromosome is in the section next to the one from which the sketch was made.

FIG. 5. Fillbasket × Debarbieux. Nuclear plate of the last sporogenous division. Six chromosomes are associated in pairs.

FIG. 6. Fillbasket × Debarbieux. Anaphase of last sporogenous division showing a pairing of the chromosomes.

FIG. 7. Fillbasket × Debarbieux. Early reconstruction stage in last sporogenous division, showing the fusing of the pairs of chromosomes at their polar ends; three chromosomes are in the adjoining section. The connecting chromatin is exaggerated in the sketch.

FIG. 8. Fillbasket × Debarbieux. Same division as the preceding; the connecting ring of chromatin does not become reticulated as early as the remainder of the chromosomes.

FIG. 9. Fillbasket × Debarbieux. Same division as the preceding sketch; shows fusing of chromosomes at the polar ends.

FIGS. 10–14. Fillbasket × Debarbieux. Figs. 10–12 are sketches of metaphase of sporogenous division, *probably not the last one*, and figs. 13 and 14 are anaphases of two similar divisions. These do not show pairing of the chromosomes.

PLATE 18

FIGS. 15–17. Express × Serpette. Prophase of the first maturation mitosis, heterotype rings.

FIGS. 18, 19. Fillbasket × Debarbieux. Metaphase of the first maturation division.

FIG. 20. Fillbasket × Debarbieux. Chromosomes from the metaphase of the first division.

FIG. 21. Fillbasket × Debarbieux. Nuclear plate, first division, showing the reduced number, seven, of chromosomes.

FIGS. 22, 23. Fillbasket × Debarbieux. Anaphase of the first maturation mitosis; in the latter sketch one of the chromosomes has failed to divide; this was the only abnormality which was seen in the sporogeny of the pea hybrids.

FIGS. 24, 25. Fillbasket × Debarbieux. All of the chromosomes of one daughter nucleus are shown; the number of chromosomes is seven.

FIG. 26. Fillbasket × Debarbieux. Early reconstruction stage of a daughter nucleus; one chromosome is in the adjoining section. No splitting of the segments is to be seen.

FIG. 27. Fillbasket × Debarbieux. Metaphase of the second maturation division.

FIG. 28. Fillbasket × Debarbieux. Typical chromosomes from the metaphase of the second division.

FIGS. 29, 30. Fillbasket × Debarbieux. Metaphase of the second division showing the reduced number of chromosomes to be seven; the nuclei are sister nuclei.

FIG. 31. Fillbasket × Debarbieux. Resting nucleus of tetrad; shows complete resting condition.

FIG. 32. Fillbasket × Debarbieux. Metaphase of the first nuclear division of tetrad ; germination of microspore.

FIG. 33. Fillbasket × Debarbieux. Reconstruction of the vegetative and the generative nuclei in first mitosis of tetrad nucleus.

PLATE 19

FIG. 34. Express, pure race. (Reduced.)

FIG. 35. Serpette, pure race. (Reduced.)

FIG. 36. Express × Serpette, showing Express reversion. (Reduced.)

FIG. 37. Express × Serpette, showing Serpette reversion. Both of the figures of Express × Serpette were drawn from plants selected at random. They are representative second generation forms. (Reduced.)